Internal and External Structures of the Head
of 3rd instar Larvae of *Amphizoa lecontei* Matthews
(Coleoptera: Amphizoidae).
A Contribution towards the Clarification
of the Systematic Position of Amphizoidae

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With 8 figures

Summary

1.) Internal and external structures of the head of 3rd instar larvae of *Amphizoa lecontei* Matthews 1872 were examined and interpreted phylogenetically.

2.) The presence of strongly developed, complex ventral pharyngeal dilator muscles is considered as a possible synapomorphy of Trachypachini and Hydradephaga excl. Gyrinidae.

3.) Caudal tentorial arms, the complete loss of the lacinia, and the origin of the galea from the unsclerotized mesal side of palpomere I are considered as synapomorphies of a monophyletic unit comprising Trachypachini, Noteridae, Amphizoidae, Hygrobiidae, and Dytiscidae.

4.) Separation of the posterior tentorial grooves as found in larvae of Haliplidae, Noteridae, Amphizoidae, Hygrobiidae, and Dytiscidae is a feature which has probably evolved several times independently.

5.) The articulation of the maxilla with an elongated, flexible process of the anterior margin of the head capsule is a possible synapomorphy of Noteridae, Amphizoidae, Hygrobiidae, and Dytiscidae.

6.) The following character states are considered as synapomorphies of Amphizoidae, Hygrobiidae, and Dytiscidae: − lateral, horizontal ridge of the head capsule (RUHNAU, 1986), − elongation of the caudal tentorial arms, − multiplication of labral setae (RUHNAU, 1986), − broad, strongly sclerotized inflected part of the labrum (secondarily modified in *Hygrobia*; RUHNAU, 1986), − loss of the mandibular retinaculum, − mandibular adductor tendon divided (RUHNAU, 1986), − cardo reduced to a small rectangular sclerite (RUHNAU, 1986), − presence of a strongly developed, broad dorsal postpharyngeal dilator muscle.

7.) The shifting of the tentorial bridge towards the posterior part of the caudal arms and the strong elongation of antennomere I (RUHNAU, 1986) are considered as synapomorphies of Hygrobiidae and Dytiscidae.

8.) The facultative closing mechanism of the functional mouth in the larva of *Amphizoa lecontei* is considered as a preceeding stage to the permanent closing mechanism in larvae of Dytiscidae excl. Copelatini.

9.) The pubescence of lateral parts of the head capsule, reduction of antennomere IV, the reduction of the sensorial appendage of the antenna, and the exchanged areas of origin of the tentoriopremental muscles are considered as autapomorphies of Amphizoidae.

10.) The following characters of amphizoid larvae are assigned to the groundplan of Adephaga: − 2 mesal mandibular edges, − presence of M. tentorio-cardinalis, − 3 premental retractor muscles, − moderately long prepharynx, − well developed hypopharynx, − wide pharynx.

11.) The monophyly of Trachypachini + Noteridae + Amphizoidae + Hygrobiidae + Dytiscidae; − of Noteridae + Amphizoidae + Hygrobiidae + Dytiscidae; − of Amphizoidae + Hygrobiidae + Dytiscidae is supported by the results of this study. − Hygrobiidae are probably the sister-group of Dytiscidae.

12.) The results of this study suggest that Gyrinidae are n o t closely related to Trachypachini and the remaining Hydradephaga.

Zusammenfassung

1. Innere und äußere Strukturen des Kopfes der Larve von *Amphizoa lecontei* Matthews 1872 (3. Stadium) wurden untersucht und phylogenetisch interpretiert.

2. Das Vorhandensein von stark entwickelten, mehrbündeligen ventralen Pharynxdilatatoren wird als mögliche Synapomorphie der Trachypachini und Hydradephaga (außer Gyrinidae) gedeutet.

3. Folgende Merkmale werden als Synapomorphien einer monophyletischen Gruppe bestehend aus Trachypachini, Noteridae, Amphizoidae, Hygrobiidae und Dytiscidae gedeutet: − Vorhandensein caudaler Tentorialarme, − völliger Verlust der Lacinia, − Insertion der Galea auf der unsklerotisierten Medianseite des ersten Palpengliedes.

4. Die Trennung der hinteren Tentorialgruben bei den Haliplidae, Noteridae, Amphizoidae, Hygrobiidae und Dytiscidae stellt ein Merkmal dar, das vermutlich mehrfach konvergent entstanden ist.

5. Die Gelenkung der Cardo mit einem langgestreckten, beweglichen Fortsatz des Vorderrandes der Kopfkapsel wird als mögliche Synapomorphie der Noteridae, Amphizoidae, Hygrobiidae und Dytiscidae gewertet.

6. Folgende Merkmale sind Synapomorphien der Amphizoidae, Hygrobiidae und Dytiscidae: − seitlicher, horizontaler Kiel der Kopfkapsel (RUHNAU, 1986), − Verlängerung der caudalen Tentorialarme (RUHNAU, 1986), − Vervielfachung der Anzahl der labralen Setae (RUHNAU, 1986), − Verbreiterung und starke Sklerotisation des eingeschlagenen Labralanteiles (sekundär abgewandelt bei *Hygrobia*; RUHNAU, 1986), − Verlust des Retinaculum der Mandibel, − Adduktorsehne der Mandibel gespalten (RUHNAU, 1986), − Cardo zu einem kleinen, rechteckigen Skleritstück reduziert (RUHNAU, 1986), − Vorhandensein eines kräftigen, breiten, dorsalen Dilatator des Postpharynx.

7. Die Verschiebung der Tentorialbrücke auf die caudalen Tentorialarme und die starke Verlängerung des ersten Antennengliedes werden als Synapomorphien der Hygrobiidae und Dytiscidae gewertet.

8. Der fakultative Verschlußmechanismus der funktionalen Mundöffnung der Larve von *A. lecontei* wird als Vorstufe zum permanenten Verschlußmechanismus der Dytiscidae (außer Copelatini) interpretiert.

9. Die Behaarung der seitlichen Teile der Kopfkapsel, die Reduktion des 4. Antennengliedes, die Reduktion des Sinnesanhangs der Antenne und die vertauschten Ursprungsflächen der tentoriopraementalen Muskeln werden als Autapomorphien der Amphizoidae gewertet.

10. Folgende Merkmale der Amphizoidae-Larven werden zum Grundplan der Adephaga gerechnet: − 2 Kanten der Mandibel-Innenseite, − das Vorhandensein von M. tentorio-cardinalis, − 3 praementale Retraktoren, − verhältnismäßig kurzer Praepharynx, − wohlentwickelter Hypopharynx, − weitlumiger Pharynx.

11. Die Monophylie der folgenden Gruppierungen wird durch die Ergebnisse dieser Studie nahegelegt: − Trachypachini + Noteridae + Amphizoidae + Hygrobiidae + Dytiscidae; − Noteridae + Amphizoidae + Hygrobiidae + Dytiscidae; − Amphizoidae + Hygrobiidae + Dytiscidae. − Die Hygrobiidae sind wahrscheinlich die Schwestergruppe der Dytiscidae.

12. Diese Untersuchung bestätigt, daß die Gyrinidae n i c h t nahe mit den Trachypachini und den anderen Hydradephagen-Gruppen verwandt sind.

Contents

1. Introduction

The family Amphizoidae was erected in 1853 by LECONTE, and a position between Carabidae and Dytiscidae was assigned to the paradoxical taxon. Indeed, larval and adult members of Amphizoidae are ambivalent in their lifestyle as well as in their morphological features (EDWARDS, 1950). The importance of this group for the understanding of evolutionary processes involving changes from terrestrial to aquatic habitats is self-evident. Hypotheses concerning the systematic position based on cladistic methods have been presented by BURMEISTER (1976), BAEHR (1979), KAVANAUGH (1986), RUHNAU (1986), and BEUTEL (1988). RUHNAU's analysis of the hydradephagan phylogeny (1986) includes various valuable interpretations of amphizoid structures. However, a detailed description of amphizoid larvae is wanting at present, and some of RUHNAU's interpretations have to be revised due to newly acquired information, especially on larvae of *Trachypachus*. The results of this study may provide a better basis for a systematic placement of Amphizoidae and a contribution towards the reconstruction of the adephagan groundplan.

2. Material, methods and abbreviations

2.1. Material

Larval specimens of *Amphizoa lecontei* Matthews were collected at Bridger Creek (1460 m), Gallatin Co., Montana (D. L. GUSTAFSON, coll.).

Specimens of *Trachypachus holmbergi* Mannerheim (Trachypachidae), *Metrius contractus* Eschscholtz, *Opisthius richardsoni* Kirby (preserved in ethanol), *Carabus coriaceus* L., *Omophron variegatum* Olivier, *Licinus silphoides* Rossi (preserved in FAE) and *Broscus cephalotes* L. (preserved in ethanol) (Carabidae) were examined for outgroup comparison.

2.2. Methods

Specimens were preserved in ethanol. Mouthparts were imbedded in Histoplast S and microtome sections were cut at 5 μm. The sections were stained with haemalaun and eosin. Some minor muscular features (see morphological results) could not be clarified due to lack of specimens which were preserved in Bouin's or FAE (formol-ethanol-acetic acid).

2.3. Abbreviations

Ad   adnasalia
An   antenna
aTa anterior tentorial arm
C   cardo
Cer cerebrum
Cs   coronal suture
cTa caudal tentorial arm
dTa dorsal tentorial arm
F   function
Fs   frontal suture
Ga   galea

Gu   gula
Hy   hypopharynx
M   mandible
Mt   mentum
Mx   maxilla
Peb   preepipharyngeal bulge
Plb   palpus labialis
Pm   prementum
Pmx   palpus maxillaris
Po   postocciput
Poa   postoccipital apodeme
pTa   posterior tentorial arms
pTg   posterior tentorial grooves
Sbg   suboesophageal ganglion
St   stipes
Ste   stemma
Tb   tentorial bridge.

3. Morphological results

3.1. Head capsule

#### 3.1.1. General appearance, external structures (Figs. 1–3)

The head of 3rd instar larvae of *Amphizoa lecontei* is large in relation to body size, broad, somewhat hexagonal in outline, and only slightly compressed dorsolaterally. The colour varies from light to darker brown, apparently depending on the age of the larvae. The mouthparts are in a prognathous position. The head is only very slightly overlapped by the prothorax dorsally. The cervical membrane is exposed ventrally, unless the head is strongly bent downwards. The extensive foramen occipitale is oval in outline.

The anteromedian sclerite of the head capsule, which is bordered by the frontoclypeal suture posteriorly, is probably composed by the frons, clypeus, and true labral parts. No traces of sutures separating these regions are present. The whole sclerite (it will be referred to as frontoclypeolabral apotome in agreement with HINTON, 1963) is rather modest in size in larvae of *A. lecontei*. The part anterior to the antenna, the clypeolabral region, is moderately long, and slightly converging anteriorly. The anterior margin is characterized by rounded adnasalia which are densely set with fine hairs along their mesal margin, and a broad, very slightly convex median section, which is totally devoid of nasal teeth. The posterior part of the frontoclypeolabral apotome, the frontal region, is about as long as the part of the head capsule posterior to it.

The frontal sutures run almost parallel in their anteriormost section and converge sligthly in the intermediate section. The posteriormost parts are strongly converging and continuous with the coronal suture posteriorly.

The well developed stemmata are arranged in two oblique rows, posterior to the antennal insertion. A distinct horizontal ridge starts immediately behind the posterior row of stemmata, and obliterates shortly before it reaches the posterolateral margin of the head capsule. Postorbital ridges (Hinteraugenleiste; TRÖSTER, 1987), or epicranial ridges (TRÖSTER, 1987) are absent.

The hind margin of the head capsule is formed by a narrow postocciput, which is bordered by a distinct postoccipital suture.
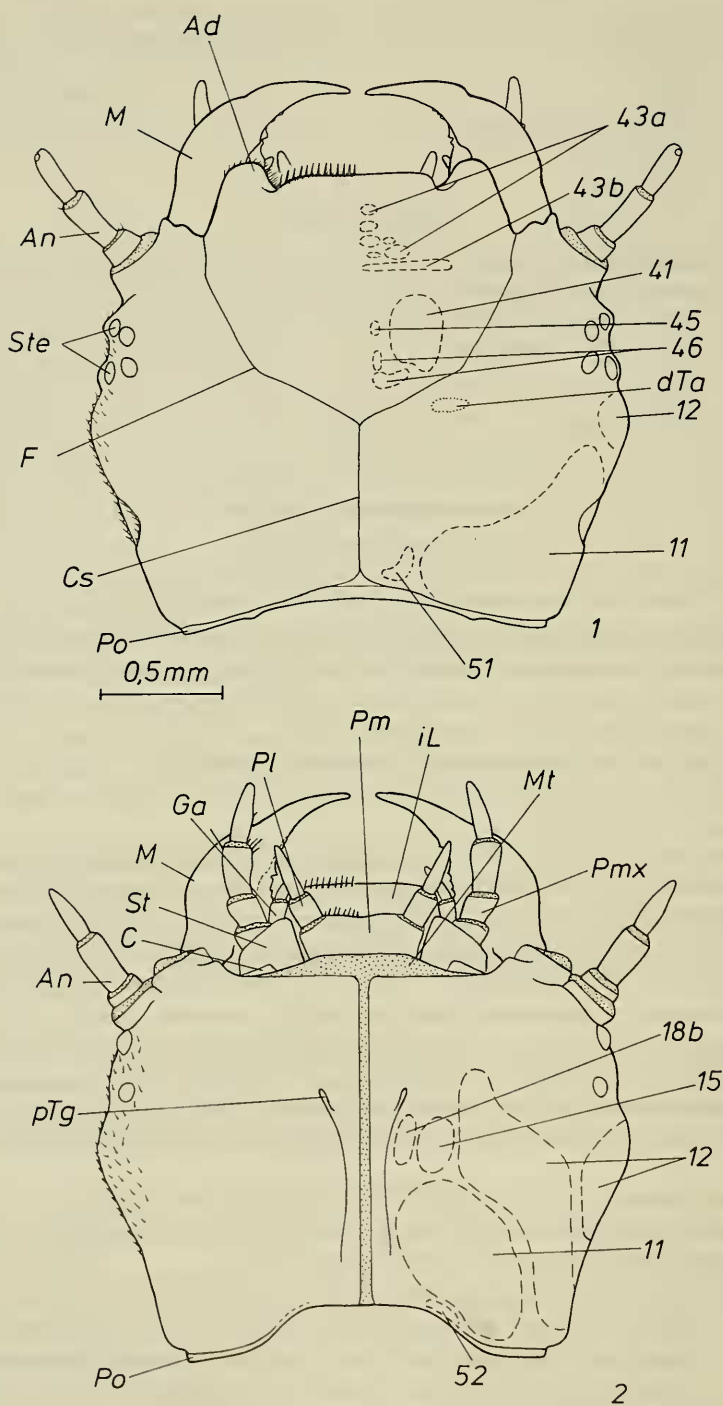
Figs. 1–2. *Amphizoa lecontei*; head, muscle attachments indicated by interrupted lines. – 1. Dorsal view. – 2. Ventral view.

The ventral wall of the head capsule is divided by a fairly broad, median membranous zone. The distinctly separated posterior tentorial grooves which define the anterior margin of the gular area, are on a level with the posterior row of stemmata. Posteriorly, they are continuous with faintly impressed lines which nearly reach the hind margin of the ventral wall of the head capsule. These lines do not correspond with distinct internal ridges, and it is unclear whether they are true gular sutures.

3.1.2. Tentorium (Figs. 2, 4)

The posterior tentorial arms which arise from the posterior tentorial grooves, are distinctly separated at their base, flat and moderately broad. Posteroventrally directed apodemes which originate from the hind margin of the posterior tentorial arms nearly reach the posterior margin of the head capsule. They are broad at their base but strongly tapering caudally. The slightly curved, moderately broad tentorial bridge arises from the base of these caudal tentorial arms. The broad dorsal tentorial arms are attached to the dorsal wall of the head capsule by means of fibrillar structures. The extremely thin anterior tentorial arms originate between the antennal base and the secondary mandibular joint.

3.2. Appendages of the head and their musculature

3.2.1. Labrum (Figs. 1, 4, 9)

The labrum is totally integrated into the frontoclypeolabral apotome as in other adephagan larvae. There is good reason to assume that the anterior margin of this composed sclerite, anterior to the origin of clypeal muscles is of true labral origin. Complete reduction of the labrum and functional replacement by the anterior clypeal margin cannot be supported by any conclusive evidence as already figured out by RUHNAU (1986). The anterior edge of the labral region is set with a row of 26 setae or labral pegs (RUHNAU, 1986). A broad, strongly sclerotized, vertical section is adjacent with the anterior edge. The lower margin of this inflected part of the labrum is bordered by a dense fringe of hairs.

Musculature: No labral muscles are present.

3.2.2. Antenna (Figs. 1–2)

The short antenna, which is composed by three distinct segments only, is inserted on a conspicuous prominence anterior to the cranial row of stemmata. Antennomere I is wider than it is long; antennomere II is more than twice as long as antennomere I, and slightly longer than antennomere III. Antennomere IV is reduced to an inconspicuous, extremely flat cupola shaped elevation. A sensorial appendage is not present.

Musculature (Fig. 9)

M. 1; M. tentorioscapalis anterior:
M. 1 originates from the proximal part of the dorsal tentorial arm and is inserted on the anterior margin of the scapal base. This muscle is slender and flattened proximally as are the following two muscles. − Function: Protractor of the antenna.
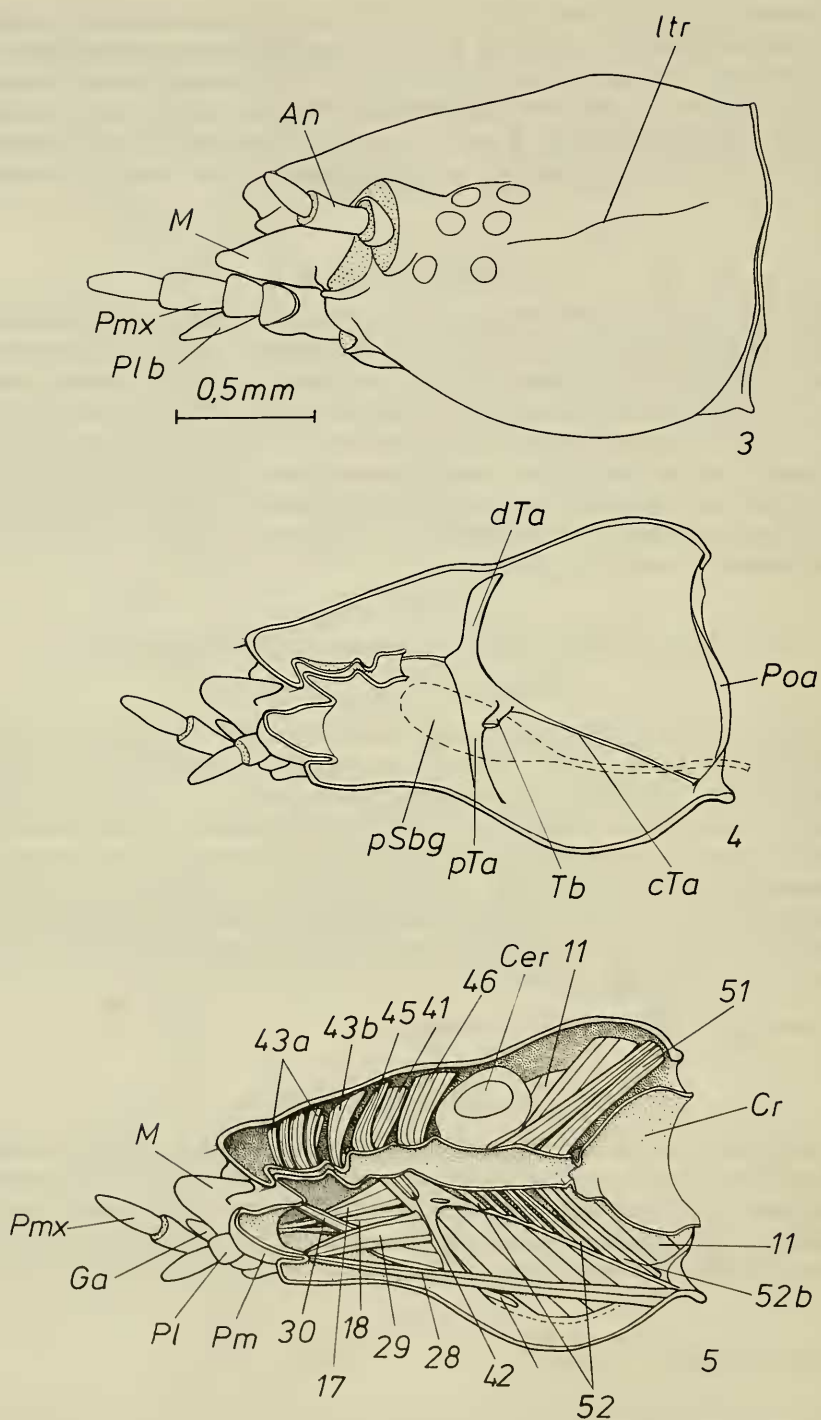
Figs. 3–5. *Amphizoa lecontei*; head. — 3. Lateral view. — 4. Sagittal section, muscles removed. — 5. Sagittal section.

M. 2; M. tentorioscapalis posterior:
M. 2 originates from the dorsal tentorial arm, posterior to M. 1, and is inserted ventrally on the scapal base. − F: Depressor of the antenna.

M. 4; M. tentorioscapalis medialis:
M. 4 originates from the dorsal tentorial arm, dorsad of M 1., and is inserted dorsally on the scapal base. − F: Levator of the antenna.

3.2.3. Mandibles (Figs. 6a, b)

The mandible is moderately long, slender in its distal part and broadening towards the base. A deep mesal groove is delimited by two sharp cutting edges. The lower cutting edge is denticulate. The mesal groove opens out into a shallow furrow on the dorsal side of the mandible. A rounded prominence at the proximal end of the ventral cutting edge is densely covered with extremely short bristles. The outer edge of the mandibles is approximately semicircular and slightly bulging in the proximal half. A distinct retinaculum is not developed. The prominence at the proximal end of the ventral cutting edge may represent a vestigial retinaculum, but this interpretation remains uncertain. A penicillum is not developed. The adductor apodeme of the mandible is bifurcate. The dorsal part of the tendon is less extensive than the ventral part.

Musculature (Figs. 1−2, 5)

M. 11; M. craniomandibularis:
M. 11 is divided into two components. − **M. 11a** originates from the posterior area of the dorsal wall of the head capsule, and is inserted on the dorsal portion of the bifurcate adductor apodeme. − **M. 11b** originates from the posteromesal area of the ventral wall of the head capsule, and is inserted on the ventral portion of the adductor apodeme. − F. Both components of M. 11 function as adductors of the mandible.

M. 12; M. craniomandibularis externus:
M. 12 is unusually strong and originates from an extensive area of the ventral wall of the head capsule and from a smaller area of the lateral wall. It is inserted on the strong abductor tendon. − F: Abductor of the mandible.

3.2.4. Maxilla (Figs. 2, 7, 8)

The maxillae are short and distinctly overlapped by the anterior margin of the head capsule. The cardo is represented by a small, ventrolateral, rectangular sclerite which is integrated into the strongly sclerotized, ventral wall of the stipes. The dorsal side of the stipes is entirely flat, and formed by a tough membrane except for an elongated sclerotization of the craniomesal area. A lacinia is not developed. The galea is composed of two segments which are about equal in length. The distal segment is constricted apically.

The maxillary palp consists of four segments. The basal segment is not developed as a fully sclerotized ring, but is membranous on its mesal side. The galea originates from the proximal part of this membranous area. Palpomere II is short and stout, about as wide as long. The following two segments are distinctly longer.

Musculature (Fig. 8)

M. 15; M. craniocardinalis externus:
M. 15 originates from the ventral wall of the head capsule, posterolateral to the origin of the

posterior tentorial arms, and is broadly attached to the lateral margin of the cardo. − F: Extensor and retractor of the maxilla.

M. 17; M. t e n t o r i o c a r d i n a l i s :
M. 17 is probably represented by a broad and flat muscle which originates from the lateral side of the posterior tentorial arm, and is inserted on a membranous area of the mesal maxillary base. − F: Flexor of the maxilla.

M. 18; M. t e n t o r i o s t i p i t a l i s :
This muscle is represented by two subunits. − **M. 18a** originates from the lateral side of the posterior tentorial arm, ventrally to M. 17, and is inserted on the mesal stipital base by means of a short tendon. − F: Flexor of the maxilla. − **M. 18b** is a fairly slender muscle which originates from the ventral wall of the head capsule, lateral to the origin of the posterior tentorial arms, and is inserted dorsally on the stipital base. − F: Retractor and levator of the maxilla.

M. 23; M. s t i p i t o p a l p a l i s :
M. 23 originates from the ventral stipital wall and is inserted dorsally on the base of palpomere I. − F: Extensor of the maxillary palp.

A stipito-stipital muscle as it is found in larvae of *C. campestris*, *C. coriaceus* and *T. holmbergi* is almost certainly absent, however the poor quality of the microtome sections does not allow a final statement.

3.2.5. Labium (Figs. 2, 5, 8)

The submental area between the posterior tentorial grooves and the hind margin of the mentum is totally integrated into the ventral wall of the head capsule. The short membranous mentum extends laterally as far as the mesal edge of the cardo. The prementum is distinctly broader than it is long. It is sclerotized ventrally and laterally. The dorsal surface is membranous except for a pair of triangular sclerotizations of the anterior region. A row of dorsally directed, stiff setae is present along the anterior margin of these sclerites. A ligula is not developed. The two segmented palpi are inserted on the anterolateral edges of the prementum. The basal segment is short and stout, slightly longer than it is broad. The second segment is more elongated and slender.

Musculature (Figs. 5, 8)

M. 28; M. s u b m e n t o p r a e m e n t a l i s :
A pair of muscles which extend along the median line. They originate from the hind margin of the ventral wall of the head capsule and are attached to the base of the prementum. − F: Retractor of the prementum.

M. 29; M. t e n t o r i o p r a e m e n t a l i s i n f e r i o r :
M. 29 originates from the upper part of the mesal side of the posterior tentorial arms, and is inserted on the base of the prementum laterally to M. 28. − F: Retractor and levator of the prementum.

M. 30; M. t e n t o r i o p r a e m e n t a l i s i n f e r i o r :
M. 30 has its origin on the mesal side of the posterior tentorial arm ventral to M. 29, and is inserted dorsolaterally on the base of the prementum.

A premento-stipital muscle is probably present but the poor quality of the microtome sections does not allow a final statement.
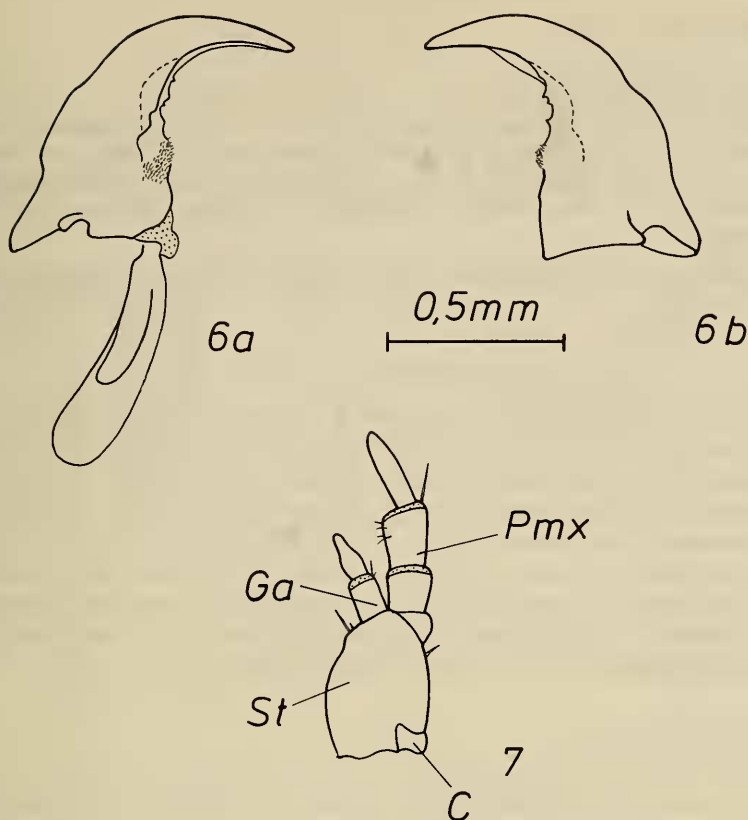
Figs. 6–7. *Amphizoa lecontei*; mouthparts. – 6a. Mandible with adductor tendon, dorsal view. – 6b. Mandible, ventral view. – 7. Maxilla, ventral view.

3.3. Preoral cavity

3.3.1. Epipharynx (Figs. 5, 9)

The tough membrane of the moderately broad, anterior part of the epipharynx (preepipharynx), forms the roof of the cranial cibarial region, which is not fused with the hypopharynx laterally. The cranialmost section, which is adjacent to the vertical, inflected part of the labrum, is steeply ascending. It fits closely together with the anterior hypopharyngeal margin, thus providing an efficient, facultative closing mechanism of the functional mouth (SNODGRASS, 1935). This preepipharyngeal section is separated from the posterior region by an inconspicuous fold. The posterior margin of the preepipharynx is distinctly bordered by a broad, transverse bulge which is set with numerous extremely short hairs. This bulge closely fits together with a corresponding bulge of the hypopharynx.

The caudal epipharyngeal section (postepipharynx) is laterally fused with the caudal part of the hypopharynx, thus forming a closed, prepharyngeal channel. This section is short, and oval in cross section. It is laterally reinforced by a strong sclerotization (hypopharngeal suspensoria).

Musculature (Figs. 1, 5):

M. 43; M. clypeopalatalis:
This muscle is divided into two sections. — **M. 43a:** This complex muscle is composed of six bundles which arise from the mesal clypeal region and are successively attached to the preepipharyngeal wall. — F: Dilators of the anterior prepharynx. — **M. 43b** arises from a fairly narrow, transverse attachment area on the middle region of the frontoclypeolabral apotome, and is inserted over the whole width of the posterior, preepipharyngeal bulge. — F: Dilator of the prepharynx.

Transverse muscle fibres extend between either side of the preepipharyngeal bulge.

3.3.2. Hypopharynx (Figs. 5, 8)

The hypopharynx is separated from the dorsal wall of the prementum by a deep membranous fold. The anteromesal and lateral parts of the anterior prehypopharynx (not fused with the epipharynx laterally) is lightly sclerotized. The central area is membranous. A distinct, posterior prehypopharyngeal bulge and an adjacent transverse depression of the anterior margin of the posthypopharynx (fused with the epipharynx) fit together with the epipharyngeal bulge. The central membranous prehypopharyngeal area, the posterior bulge, and the anterior part of the adjacent depression are covered with numerous, extremely short hairs. The posthypopharynx is short and reinforced by the strongly sclerotized suspensoria.

Musculature (Figs. 1, 5, 8)

M. 41; M. frontohypoharyngalis:
A powerful muscle, which originates from a fairly extensive area of the posterior frontal region and is attached to the apex of the suspensoria. — F: Retractor of the mouth angle.

M. 42; M. tentoriohypopharyngalis:
A short muscle band which originates from the mesal side of the posterior tentorial arm, and is inserted on the posterolateral margin of the hypopharynx. — F: Keeps the prepharynx in position.

A pair of muscles originates from the posteromesal margin of the hypopharynx and is inserted on the posteromesal region of the pharynx.

3.4. Pharynx (Fig. 5)

The pharynx is fairly long and wide. It is separated by a fold from the extremely spacious crop.

Musculature

M. 45; M. frontobuccalis anterior:
M. 45 originates from the frontal region, close to the median line and is inserted on the dorsal pharyngeal wall, posterior to the epipharyngeal bulge. — F: Dilator of the pharynx.

M. 46; M. frontobuccalis posterior:
A strong muscle which arises from the posteromesal region of the frons and is inserted on the dorsal pharyngeal wall, anterior to the brain. — F: Dilator of the pharynx.

M. 51; M. verticopharyngalis:
M. 51 is composed of two broad, flat muscle bundles, which arise from the posterolateral
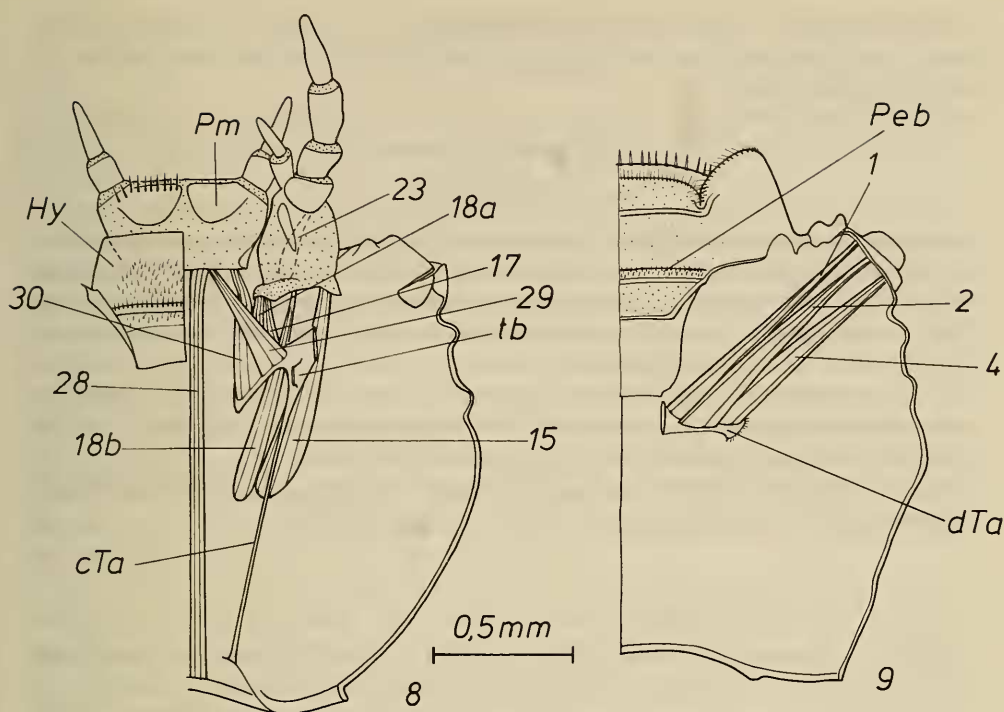
Figs. 8−9. *Ampizoa lecontei*; head. − 8. Horizontal section, ventral part. − 9. Horizontal section, dorsal part.

margin of the dorsal wall of the head capsule and are inserted dorsolaterally on the posterior pharynx. − F: Dilator of the posterior pharynx.

M. 52; M. tentoriopharyngalis:
A complex muscle which arises from the base of the tentorial bridge, from the posterior tentorial process, and from the ventrolateral margin of the ventral wall of the head capsule. All bundles of M. 52 are inserted on the ventral side of the posterior pharynx.

3.5. Crop and crop contents (Fig. 5)

An extremely wide crop is posteriorly adjacent to the pharynx. A membranous fold clearly defines the border between both parts of the alimentary channel.

No sclerotized parts were found in the crop. The food substances are of a more or less homogenous, curd-like consistency.

4. Discussion of selected characters

The determination of the polarity of character states is based on the outgroup comparison method (WATROUS & WHEELER, 1981). A broad spectrum of taxa is taken into consideration in order to avoid misinterpretation. The outgroup includes Gyrinidae which are the sister-group of the remaining Adephaga according to BEUTEL & ROUGHLEY (1988), Trachypachini, Haliplidae, Noteridae, and various

taxa which belong to a basal stock of Geadephaga[1]) (e. g. *Metrius, Carabus*). Additionally, polyphagan larvae are taken into consideration for the interpretation of some muscular features.

4.1. Head capsule

4.1.1. Lateral ridge

A temporal, horizontal ridge, as it is found in larvae of *A. lecontei*, is also present in 1st instar larvae of *Hygrobia*, and most larvae of Dytiscidae according to RUHNAU (1986). This character state is considered apomorphic in agreement with RUHNAU (1986), and the partial or complete reduction as a secondary feature in case of L_{2-3} of *Hygrobia*, and some dytiscid larvae.

The plesiomorphic condition, i. e. absence of the horizontal ridge, is found in other hydradephagan larvae, in larvae of *Trachypachus* (RUHNAU, 1986), and in other geadephagan larvae (THOMPSON, 1979; personal observation).

The presence of the horizontal ridge is probably a derived groundplan feature and synapomorphy of Amphizoidae, Hygrobiidae and Dytiscidae.

4.1.2. Posterior tentorial grooves and gular area

Distinctly separated posterior tentorial grooves are found in larvae of Amphizoidae, Hygrobiidae, Dytiscidae, Haliplidae, and Noteridae (BERTRAND, 1972).

The posterior tentorial grooves are adjacent in larvae of Gyrininae[2]) (NOARS, 1956; STAHL, 1984), *T. holmbergi*, and in other geadephagan larvae with very few exceptions (*Loricera, Licinus*, pers. obs.). This is almost certainly a groundplan feature of Adephaga. The closely adjacent posterior tentorial grooves of gyrinid larvae are not considered as a secondary feature, as suggested by RUHNAU (1986).

Separated posterior teritorial grooves have probably evolved several times.

4.1.3. Setation

The presence of dense fields of very short setae, which are inserted on small tubercles on the lateral area of the head capsule of *A. lecontei* is almost certainly apomorphic. A somewhat similar condition is found in haliplid larvae (SEEGER, 1971). However, the setae are less numerous and longer than in larvae of *A. lecontei*. The tubercles are regularly distributed and most of them are devoid of setae. A more or less smooth surface structure is found in larvae of other hydradephagan families and larvae of Geadephaga. This is certainly the groundplan condition of Adephaga.

The character state which is found in amphizoid larvae is considered as an autapomorphic feature of the family.

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[1]) The use of the terms Geadephaga and Hydradephaga does not imply that these groups are monophyletic.

[2]) The larvae of Spanglerogyrinae are yet unknown.

4.2. Tentorium

4.2.1. Caudal arms

Caudal tentorial arms are present in larvae of *Amphizoa, Hygrobia* and Dytiscidae (Ruhnau, 1986) and also in larvae of *T. holmbergi*. This is almost certainly a derived feature.

Caudal tentorial arms are absent from larvae of Gyrininae (Noars, 1956; Stahl, 1984) and from the geadephagan larvae (excl. *Trachypachus*) which have been examined so far [*Carabus coriaceus* L., *Omophron variegatus* Olivier, *Broscus cephalotes* L., personal observation; *Cicindela campestris* L., Breyer, 1989; *Pterostichus nigrita* (Paykull), Tröster, 1987]. Consequently the absence is considered plesiomorphic and a groundplan character state of Adephaga.

The base of the posterior tentorial arms is expanded in larvae of *H. lineatocollis* (Beutel, 1986), and two short posterior processes are present in larvae of *Noterus crassicornis* (Ruhnau, 1985). The posterior tentorial grooves of larvae of *N. crassicornis* (other noterid larvae?) are shifted to the posterior margin of the head capsule (Ruhnau, 1985). This highly derived condition may have caused the replacement of one elongate caudal arm by two short processes.

As a working hypothesis, the presence of caudal tentorial arms is considered as a derived groundplan feature and synapomorphy of Trachypachini, Noteridae, Amphizoidae, Hygrobiidae and Dytiscidae. This implies that the caudal arms are secondarily shortened in *N. crassicornis*. The condition which is found in *H. lineatocollis* is considered as a preceeding stage.

4.2.2. Elongation of the caudal arms

The caudal tentorial arms are strongly elongated in larvae of *A. lecontei, Hygrobia* (Ruhnau, 1986) and Dytiscidae (De Marzo, 1979). It is selfevident that this character state is apomorphic. It is considered as a synapomorphy of Amphizoidae, Hygrobiidae and Dytiscidae.

4.2.3. Tentorial bridge

The tentorial bridge of amphizoid larvae does not arise from the posterior part of the caudal arms as stated by Ruhnau (1986), but from their broad, basalmost section. This position is close to the groundplan condition of Adephaga, i. e. origin of the tentorial bridge from the posterior arms (*T. holmbergi*; personal observation).

The dislocation of the tentorial bridge towards the posterior part of the caudal arms could be considered as a significant synapomorphy of Hygrobiidae and Dytiscidae if this character state is found in larvae of *Hygrobia*.

4.2.4. Anterior tentorial arms

The anterior tentorial arms are extremely thin in larvae of *Amphizoa* and Dytiscidae (De Marzo, 1979). This is almost certainly a derived condition.

Strong anterior arms are present in larvae of Gyrininae (Noars, 1956; Stahl, 1984), *T. holmbergi*, and other geadephagan larvae (Breyer, 1989; Tröster, 1987).

The phylogenetic interpretation of this character depends on the condition which is found in larvae of *Hygrobia* which have not been examined so far.

4.3. Labrum

4.3.1. Labral setae

The multiplication of labral setae or pegs [*Amphizoa:* 2 + 24 in L_{1-3}, *Hygrobia:* 2 + 12 in L_1, 2 + 24 in L_{2-3}, *Copelatus* (Dytiscidae): 2 + 12 in L_1, 2 + 24 in L_2, 2 + 36 in L_3; Ruhnau, 1986] is considered apomorphic in agreement with Ruhnau (1986). The presence of 2 pairs of labral setae as found in larvae of Gyrininae and *Trachypachus* (Ruhnau, 1986) is considered as a groundplan character state of Adephaga.

The multiplication of labral setae is probably a synapomorphy of Amphizoidae, Hygrobiidae and Dytiscidae as suggested by Ruhnau (1986).

4.3.2. Inflected part

A broad, strongly sclerotized, inflected part of the labrum is present in larvae of *A. lecontei* and Dytiscidae (De Marzo, 1979). Captured prey is pressed against this specialized part of the labrum by the mandibles (Korschelt, 1924; Bertrand, 1928; Ruhnau, 1986). This is almost certainly an apomorphic condition.

A fairly narrow sclerotized, inflected part of the labrum is found in larvae of Gyrininae (Noars, 1956; Stahl, 1984), Haliplidae (Jaboulet, 1960; Beutel, 1986), and *T. holmbergi*. There is no direct interaction between the labrum and the mandibles. This condition is considered as a groundplan character state of Adephaga. The sclerotized, inflected part of the labrum is broad in *N. crassicornis* (Ruhnau, 1985), but there is no interaction with the mandibles as described above.

The character state which is found in larvae of *A. lecontei* and Dytiscidae is interpreted as a derived groundplan feature and synapomorphy of Amphizoidae, Hygrobiidae, and Dytiscidae by Ruhnau (1986). This implies that the narrow inflected part of the labrum of hygrobiid larvae is a secondary condition. Such an assumption is quite plausible, as the highly specialized oligochaet-feeding habits of hygrobiid larvae have obviously resulted in many highly autapomorphous features of the mouthparts and preoral cavity.

4.4. Antenna

4.4.1. Antennomere I

Antennomere I is short in larvae of *A. lecontei* as in larvae of Gyrinidae, Haliplidae, Noteridae (Bertrand, 1972) and *T. holmbergi*. This is a groundplan character state of Adephaga.

Antennomere I is at least twice as long as it is wide in larvae of *Hygrobia* and Dytiscidae (Ruhnau, 1986). The latter condition is doubtless apomorphic, and is considered as a synapomorphy of Dytiscidae and Hygrobiidae in agreement with Ruhnau (1986).

4.4.2. Antennomere IV

Antennomere IV is extremely reduced in larvae of *A. lecontei*. This is certainly an apomorphic condition.

Antennomere IV is only slightly smaller than the preceeding antennomere in larvae of Gyrinidae (Bertrand, 1972) and *T. holmbergi*. This is considered as an adephagan groundplan character state.

Antennomere IV is moderately reduced in size in larvae of Noteridae (UÉNO, 1957; BERTRAND, 1972; RUHNAU, 1985), and strongly reduced in larvae of Haliplidae, Hygrobiidae, and Dytiscidae (BERTRAND, 1972). The decrease in size of antennomere IV is a gradual modification, which may have occurred several times independently.

The extreme reduction of antennomere IV in larvae of *Amphizoa* is an autapomorphy of the family.

4.4.3. Sensorial appendage of antennomere III

The absence of the sensory appendage from antennae of *A. lecontei* is certainly an apomorphic feature.

A distinct sensory appendage is present in larvae of *T. holmbergi*, Haliplidae (JABOULET, 1960), Hygrobiidae and Dytiscidae (BERTRAND, 1972). This is considered as a groundplan feature of Adephaga or of Adephaga excl. Gyrinidae, depending on whether the absence from the antennae of gyrind larvae (NOARS, 1956; BERTRAND, 1972) is primitive or a secondary feature.

The sensorial appendage is also reduced in larvae of Noteridae (BERTRAND, 1972; RUHNAU, 1985). A subapical, membranous sensory field on antennomere III of *N. crassicornis* is interpreted as a remnant by RUHNAU (1985).

The absence of the sensory appendage is considered as an autapomorphous character state of Amphizoidae. The reduction in larvae of Noteridae is almost certainly a result of parallel evolution.

4.5. Mandible

4.5.1. Retinaculum

The mandibular retinaculum is strongly reduced in larvae of *A. lecontei*, Gyrininae, Hygrobiidae and Dytiscidae (BERTRAND, 1972). A small denticle on the mesal side of the mandible of larvae of *Gyrinus* (BERTRAND, 1972; STAHL, 1984) and the pubescent elevation of the mandibles of larvae of *A. lecontei* may represent vestigial retinacula. The reduction is certainly an apomorphic feature.

The presence of a strongly pronounced retinaculum in larvae of *T. holmbergi* and other geadephagan larvae (THOMPSON, 1979) and in larve of Noteridae (UÉNO, 1957; BERTRAND, 1972) is certainly a groundplan character state of Adephaga. A tendency towards reduction is found in haliplid larvae but the retinaculum is still distinct in most species (SEEGER, 1971; BERTRAND, 1972).

The reduction of the retinaculum is considered as a synapomorphy of Gyrininae or Gyrinidae on one hand and as a synapomorphy of a monophyletic unit comprising Amphizoidae, Hygrobiidae, and Dytiscidae on the other hand. As a reduction which is closely correlated with functional aspects of feeding (crushing the prey against the inflected part of the labrum, RUHNAU, 1986; sucking mandibles), this character should not be overvalued.

4.5.2. Mesal edges

Two mesal mandibular edges which enclose a more or less distinct groove are present in larvae of *A. lecontei*, *T. holmbergi*, Noteridae (in part; BERTRAND, 1972; RUHNAU, 1985), *Hygrobia* (L_1, RUHNAU, 1986), *C. haemorroidalis* (DE MARZO, 1979), and in larvae of *C. coriaceus*, *Metrius* (L_1) and *Opisthius*. From this character

distribution it appears more plausible to interpret the presence of two mesal mandibular edges as a groundplan feature of Adephaga than as an apomorphic feature as suggested by RUHNAU (1986).

As figured out by RUHNAU (1986), closed mandibular channels have evolved independently several times from a mesal groove enclosed by two cutting edges: in Gyrininae (*Spanglerogyrus*?), in Noteridae (*Hydrocanthus, Canthydrus*; RUHNAU, 1986), and in Dytiscidae excl. Copelatini. The mesal mandibular groove is much deeper in larvae of *A. lecontei* than in larvae of *T. holmbergi*. This condition may be considered a preceeding stage of the closed mandibular channel of larvae of Dytiscidae excl. Copelatini.

The loss of the dorsal edge in L_{2-3} of larvae of *H. tarda* is almost certainly a secondary, autapomorphous feature of Hygrobiidae which is correlated with extremely specialized feeding habits (RUHNAU, 1986).

4.5.3. Adductor tendon

The deeply bifurcated mandibular adductor tendon found in larvae of *A. lecontei, Hygrobia* (RUHNAU, 1986) and Dytiscidae (SPEYER, 1922; RUHNAU, 1986) is considered as an apomorphic feature in agreement with RUHNAU (1986).

No similar condition has been described for other larvae of Adephaga so far. Consequently, undivided adductor tendons have to be considered as a groundplan character state of Adephaga.

Divided adductor tendons are almost certainly a synapomorphy of Amphizoidae, Hygrobiidae and Dytiscidae as already stated by RUHNAU (1986). However, in contrast to RUHNAU (1986), no dorsolateral pharyngeal dilators pass between both branches of the adductor apodeme in larvae of *A. lecontei*. If this doubtlessly derived character state is present in larvae of *Hygrobia* (as in Dytiscidae; SPEYER, 1922), it could be considered as a significant synapomorphy of Hygrobiidae and Dytiscidae.

4.6. Maxilla

4.6.1. Articulation

The articulation of the cardo with a „finger-like, flexible cranial process" of the anterior margin of the head capsule is interpreted as a synapomorphy of *Trachypachus* and Hydradephaga by RUHNAU (1986). This is certainly a noteworthy character, however, the process is not flexible in larvae of Gyrinidae, *Copelatus* and *Eretes* (RUHNAU, 1986; interpreted as secondary feature), and fairly short and definitely not flexible in larvae of *T. holmbergi* (personal observation). Furthermore, such an articulation is not described for larvae of *Haliplus lineatocollis* by BEUTEL (1986).

As a working hypothesis, this articulation mode may be considered as a synapomorphy of Noteridae, Amphizoidae, Hygrobiidae, and Dytiscidae. However, it is evident, that this character needs further study.

4.6.2. Cardo

The cardo is reduced to a small rectangular plate, which is relatively firmly integrated into the laterobasal part of the ventral wall of the stipes in larvae of *Amphizoa, Hygrobia* and Dytiscidae (BERTRAND, 1972; RUHNAU, 1986). This is considered an apomorphic condition in agreement with RUHNAU (1986).

The presence of a ventral cardo sclerite, which extends along the whole width of the stipital base or nearly so, as it is found in larvae of Gyrininae (cardo exceptionally large; NOARS, 1956; STAHL, 1984), *T. holmbergi*, Haliplidae (JABOULET, 1960; BEUTEL, 1986), and *N. crassicornis* (RUHNAU, 1985), is considered as a groundplan feature of Adephaga.

The derived character state is a significant synapomoprhy of Amphizoidae, Hygrobiidae and Dytiscidae as already stated by RUHNAU (1986).

4.6.3. Lacinia

The lacinia is completely absent from larvae of *T. holmbergi*, Noteridae (UÉNO, 1957; RUHNAU, 1985), *Amphizoa*, *Hygrobia* and Dytiscidae (BERTRAND, 1972). This is certainly an apomorphic feature.

Elongate laciniae are characteristic for larvae of Gyrininae (BERTRAND, 1972) but are also present in larvae of *Metrius* and *Omophron*. This is probably a groundplan character state of Adephaga.

Different degrees of reduction are found in larvae of Geadephaga (THOMPSON, 1979). Highly modified laciniae are present in larvae of Haliplidae (JABOULET, 1960; BEUTEL, 1986).

The complete absence from larvae of *Trachypachus*, Noteridae, Amphizoidae, Hygrobiidae, and Dytiscidae may be considered as a possible synapomorphy of these groups. The presence of three strong hooks on the maxilla of larvae of *Copelatus* (BERTRAND, 1972) is almost certainly a secondary feature, which is correlated with the highly unusual attachment of the abductor muscle of the cardo according to RUHNAU (1986).

4.6.4. Galea

The galea is inserted on the mesal, unsclerotized side of palpomere I in larvae of *A. lecontei*, *T. holmbergi*, Noteridae (UÉNO, 1957; RUHNAU, 1985) and some members of Dytiscidae (e. g. *Matus ovatus ovatus* Leech; WOLFE & ROUGHLEY, 1985). This feature is considered apomorphic.

The galea is well separated from palpomere I in larvae of Gyrininae and the vast majority of geadephagan larvae (THOMPSON, 1979). This is certainly a groundplan character state of Adephaga.

The fusion of the walls of the galea and palpomere I in larvae of Cicindelinae (BREYER, 1989) is an autapomorphic feature which is distinctly different from the condition described above. The galea of haliplid larvae is cupola-shaped and palpomere I is completely reduced (JABOULET, 1960; BEUTEL, 1986).

The origin of the galea from the membranous mesal side of palpomere I is considered as a derived groundplan feature and synapomorphy of Trachypachini, Noteridae, Amphizoidae, Hygrobiidae and Dytiscidae. This implies that the separation of the origin of the galea from palpomere I in most larvae of Dytiscidae (BETRAND, 1972) and the complete loss of the galea in larvae of *Hygrobia* and most hydroporine larvae (BERTRAND, 1972) are secondary features.

4.6.5. Musculature

The loss of M. tentorio cardinalis is considered a synapomorphy of Amphizoidae, Hygrobiidae and Dytiscidae by RUHNAU (1986). However, M. tentoriocardinalis is present in larvae of *A. lecontei* and *Ilybius* sp. (pers. obs.), as in other adephagan larvae.

4.7. Labium

4.7.1. Premental muscles

Three premental muscles as they are found in larvae of *A. lecontei* are also present in larvae of Gyrininae (NOARS, 1956; STAHL, 1984), *Peltodytes* (RUHNAU, 1986), Noteridae, Hygrobiidae, Dytiscidae (RUHNAU, 1986) and in many polyphagan larvae (DAS, 1937). From this character distribution it appears much more plausible to consider this character state as plesiomorphic and an adephagan groundplan feature than as apomorphic as suggested by RUHNAU (1986).

The loss of M. submentopraementalis is a common derived feature of the larvae of Geadephaga (excl. Trachypachini) examined so far (TRÖSTER, 1987; BREYER, 1989; pers. obs.).

4.7.2. Arrangement of Mm. tentoriopraementales

M. tentoriopraementalis superior originates from the basal part of the posterior tentorial arm, ventrally to the origin of M. tentoriopraementalis inferior. This arrangement of premental muscles is certainly apomorphic.

M. tentoriopraementalis superior has its origin dorsal to M. tentoriopraementalis inferior in all other adephagan larvae examined. It is obvious that this condition has to be assigned to the groundplan of Adephaga.

The derived character state is probably an autapomorphic feature of Amphizoidae.

4.8. Preoral cavity

4.8.1. Size and shape of the prepharynx

The prepharynx of larvae of *A. lecontei* is fairly short, and moderately broad. This is probably a groundplan feature of Adephaga. A similar condition is found in larvae of *T. holmbergi* and in larvae of *C. haemorroidalis* (DE MARZO, 1979).

The prepharynx is very short and transformed into a broad, transverse sucking chamber in larvae of Dytiscidae excl. *Copelatus* (DE MARZO, 1979), whereas it is extremely elongated in larvae of *Orectochilus villosus* (NOARS, 1956), *Gyrinus substriatus* (STAHL, 1984), *Haliplus lineatocollis* (BEUTEL, 1986), and *N. crassicornis* (RUHNAU, 1986). The former condition is considered as a synapomorphy of Dytiscidae excl. Copelatini in agreement with RUHNAU & BRANCUCCI (1984), whereas the latter condition has almost certainly evolved several times independently. The prepharynx is only moderately long in larvae of *Dineutes* sp. (DORSEY, 1943), and the groundplan condition of Noteridae (*Phreatodytes, Notomicrus*) is not known at present.

4.8.2. Functional mouth

The postlabral, vertical epipharyngeal section and the anterior hypopharyngeal margin of larvae of *A. lecontei* provide an efficient facultative closing mechanism for the prepharyngeal opening or functional mouth. This is probably a derived condition and a preceeding stage of the highly specialized, permanent closing mechanism which is found in larvae of Dytiscidae excl. *Copelatus* (DE MARZO, 1979).

The prepharynx is closed by contact of an epipharyngeal bulge and the anterior hypopharyngeal margin in larvae of *T. holmbergi* and *C. coriaceus*. This is probably a groundplan character state of Adephaga.

The permanent closing mechanism mentioned above is almost certainly a synapomorphy of Dytiscidae excl. Copelatini. Whether the condition which is found in *A. lecontei* is a derived groundplan feature of Amphizoidae, Hygrobiidae and Dytiscidae is a matter of speculation, due to the highly autapomorphous condition of the prepharyngeal region in hygrobiid larvae.

Permanent closing mechanisms have evolved independently within Gyrininae (*O. villosus*, NOARS, 1956).

4.8.3. Hypopharynx

A well developed hypopharynx as it is found in larvae of *A. lecontei* is also present in larvae of *Gyrinus* (RUHNAU, 1986), *T. holmbergi*, Haliplidae (JABOULET, 1960; BEUTEL, 1986), *N. crassicornis* (RUHNAU, 1985), *C. haemorroidalis* (DE MARZO, 1979), *C. coriaceus*, *Nebria* sp. (SPENCE & SUTCLIFFE, 1982) and many polyphagan larvae (DORSEY, 1943; PRADHAN, 1948). Judging from this distribution of character states it is obvious that the presence of a well developed hypopharynx is a groundplan feature of Adephaga, and not a secondarily developed structure ("hypopharynx-like swelling") as suggested by RUHNAU (1986). This view is also supported by the presence of median and lateral tentorio-hypopharyngeal muscles in *T. holmbergi* and *C. coriaceus*.

The reduction of the hypopharynx is probably correlated with improved liquid feeding and has certainly taken place several times independently. A high degree of reduction is found in larvae of *O. villosus* (NOARS, 1956) and in the majority of carabid larvae (e. g. *P. nigrita*, TRÖSTER, 1987; *B. cephalotes*; *Licinus silphoides*). The hypopharynx is strongly modified in larvae of Dytiscidae excl. *Copelatus* (DE MARZO, 1979) due to the specialized closing mechanism of the functional mouth.

4.9. Pharynx

4.9.1. Shape

A wide pharynx is present in larvae of *A. lecontei* and *C. haemorroidalis*. This is probably a groundplan feature of Adephaga, as a similar condition is also found in larvae of *T. holmbergi*.

A conspicuous contrast between the narrow pharynx and the short, transverse prepharyngeal sucking chamber is characteristic for larvae of Dytiscidae excl. *Copelatus*.

The latter condition is considered as a synapomorphy of Dytiscidae excl. *Copelatus* by RUHNAU & BRANCUCCI (1984). A narrow pharynx is also found in larvae of Gyrininae (NOARS, 1956; STAHL, 1984) and in larvae of *P. nigrita* (TRÖSTER, 1987). It is quite obvious that there is a correlation between narrowing of the pharynx and advanced liquid feeding habits, either by means of mandibular sucking channels or with strongly developed prepharyngeal filter mechanisms as in „higher carabids".

4.9.2. Dorsal postpharyngeal dilators

An exceptionally broad postcerebral pharyngeal dilator muscle is found in larvae of *A. lecontei* and Dytiscidae (DE MARZO, 1979) (*Hygrobia*?). This is certainly a derived feature.

The presence of a moderately developed postcerebral dilator as found in larvae of *T. holmbergi* and *C. coriaceus* is considered as a groundplan feature of Adephaga. The muscle is absent from larvae of *O. villosus* (NOARS, 1956), *G. substriatus* (STAHL, 1984), *H. lineatocollis* (BEUTEL, 1956), *N. crassicornis* (RUHNAU, 1986), and from larvae of *Nebria* sp. (SPENCE & SUTCLIFFE, 1982), *P. nigrita* (TRÖSTER, 1987) and *L. silphoides*. The muscle is present but extremely weak in larvae of *C. campestris* (BREYER, 1989), *Leistus* sp., and *O. variegatum*.

4.9.3. Ventral pharyngeal dilators

Strong and complex ventral dilators are found in larvae of *A. lecontei* as in larvae of *H. lineatocollis* (BEUTEL, 1986), *N. crassicornis* (RUHNAU, 1986) and Dytiscidae (SPEYER, 1922). A strong ventral dilator is also present in larvae of *T. holmbergi*, however the precise shape and position could not be clarified so far due to lack of well preserved specimens. The increase in size of M. tentoriopharyngalis is probably correlated with the presence of caudal tentorial arms, or at least caudal extensions of the posterior tentorial arms (*H. lineatocollis*; BEUTEL, 1986) and is considered apomorphic.

The presence of an undivided, moderately developed M. tentoriopharyngalis as found in larvae of *C. coriaceus* is considered as a groundplan feature of Adephaga. A similar condition is found in many polyphagan larvae (DORSEY, 1943).

M. tentoriopharyngalis is absent from larvae of *O. villosus* (NOARS, 1956; the muscle designated as 'dilatateur ventral posterieur de l'atrium' by NOARS is a hypopharyngeal muscle), *G. substriatus* (STAHL, 1984), *C. campestris* (BREYER, 1989), *O. variegatum* and *L. silphoides*. It is represented by a few fibres only in *Nebria* sp. (SPENCE & SUTCLIFFE, 1982) and *P. nigrita* (TRÖSTER, 1987).

Increase in size of the ventral pharyngeal dilator muscles is considered as a possible synapomorphy of Trachypachini and Hydradephaga excl. Gyrinidae. However, parallelism cannot be excluded in this case.

4.10. Crop

An extremely wide crop is posteriorly adjacent to the pharynx in larvae of *A. lecontei* and *C. haemorroidalis*. Both parts of the digestive tract are separated by a membranous fold. This condition is not known from other larvae of Adephaga so far, and has to be considered as a derived character state. Whether it is a derived groundplan feature of Amphizoidae, Hygrobiidae and Dytiscidae is open to question.

5. Concluding remarks

The results presented in this study are in agreement with BEUTEL (1986, 1988), and with BURMEISTER (1976) and RUHNAU (1986) as far as Amphizoidae, Hygrobiidae and Dytiscidae are concerned. The monophyly of Amphizoidae, Hygrobiidae and Dytiscidae seems to be one of the few solved problems of adephagan phylogeny. A sister-group relationship between Hygrobiidae and Dytiscidae seems quite likely. There are closer affinities between larvae of Amphizoidae and Dytiscidae in terms of preoral structures, however this is probably due to the highly derived feeding habits of *Hygrobia* and correlated specialized structural features. The monophyly of Tra-

chypachini, Noteridae, Amphizoidae, Hygrobiidae and Dytiscidae is supported by three synapomorphies. A sister-group relationship between this monophyletic unit and Haliplidae is possible, but needs further support. The results of this study suggest that Gyrinidae are not closely related with Trachypachini and the remaining Hydradephaga. These interpretations are in agreement with a study by BEUTEL & ROUGHLEY (1988), which is largely based upon characters of adults.

6. Acknowledgements

7. References

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